

THE THEORY OF HABITAT SELECTION:
EXAMINED AND EXTENDED USING *PEMPHIGUS* APHIDS

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Grinnell (1914, 1922) was the first to hypothesize an ecological basis for dispersal. He concluded that since the probability of survival for dispersers was so low, "the interests of the individual are sacrificed in the interests of the species" (Grinnell 1922, p. 379). If all dispersing individuals suffer reduced fitness, however, the trait would not evolve (MacArthur 1972). Increased individual fitness should form the basis for dispersal and habitat selection. For supporting theory see Kluyver and Tinbergen (1953), Lack (1954), Levins (1962, 1968), Brown (1969), Fretwell and Lucas (1970), Fretwell (1972), Templeton and Rothman (1974), Rosenzweig (1974) and Doyle (1975).

Fretwell and Lucas (1970) and Fretwell (1972) showed that if higher densities resulted in lower individual fitness then, as individuals settled in the best habitat, a density would eventually be reached at which expected fitness in a poorer habitat would be as high as in the best habitat. At this point colonization of the poorer habitat would begin, and as population densities increased even further successively poorer habitats would be colonized. Depending upon the presence or absence of territorial behavior, two major predictions were made. With the "free distribution" all colonizers settle in the habitat of their choice. No individual can prevent another from settling and using available resources. Thus, as an additional colonizer settles, expected fitness of all established individuals is reduced by an equal amount and all have the same expected fitness. In this system, it is predicted that settling densities will be adjusted such that the average fitness in habitats of varying competitor density will be identical (fig. 1). In comparison, the "despotic distribution" assumes that the dominance and/or territoriality are behavioral traits which act to limit density within a habitat, thereby denying resources to less dominant individuals. Subdominants which succeed in entering a habitat occupy interstitial spaces between other territories or exist as floaters. Due to the disparity in resources available to individuals, expected fitnesses of colonizers within the habitat are unequal. Since territorial behavior places a limit on the number of colonizers which may become established, the theory predicts that the average fitness in the most densely occupied habitat will be greater than the average fitness

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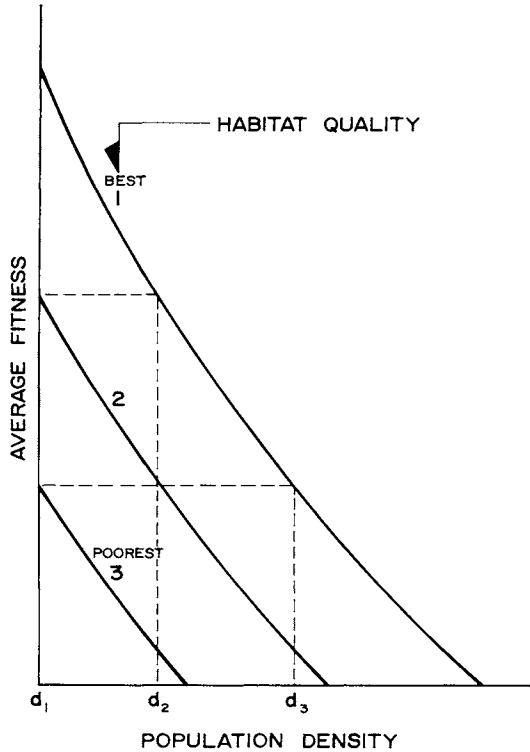


FIG. 1.—Assuming that fitness is negatively correlated with competitor density, the horizontal dashed lines show that as competitor density increases in the best habitat (1), colonization of poorer habitats (2 and 3) becomes favorable, but only at reduced densities. Figure adapted from Fretwell and Lucas (1970) and MacArthur (1972).

in habitats with fewer competitors. These predictions assume that individuals can accurately assess and integrate variables such as habitat quality and competitor density. Additionally, there are energetic and time constraints which limit the period of searching and determine the maximum time period during which a decision must be made. Unfortunately these hypotheses are largely untested (Fretwell 1972, p. 107–112) because the difficulties of measuring individual fitness in habitats of known quality are enormous (see also Wiens 1976). However, relative fitness of the gall-forming aphid, *Pemphigus betae* Doane, which produce all progeny in a single gall, can be readily assessed. Even abortive attempts (i.e., zero fitness) at gall formation are visible.

The stem mothers of *Pemphigus betae* emerge from eggs which overwinter in the deeply fissured bark of the main branches and trunk of narrowleaf cottonwood, *Populus angustifolia*, and migrate en masse to immature leaves where their feeding activities stimulate production of a hollow gall. Emergence and migration of stem mothers, each measuring about .6 mm in length, is precisely synchronized with bud burst. Within the confines of the gall a mature stem mother parthenogenetically and vivipariously produces up to 275 progeny. In midsummer

the gall dehisces and winged adults migrate to a secondary host. In the fall another generation of winged migrants returns to the primary host where $2N$ females and $2N-1$ males are produced. After mating the female lays a single egg, completing the life cycle.

Whitham (1978) showed that the size of the mature leaf is critical to the ultimate fitness of the colonizing stem mother. Field experiments and other observations indicate that large leaves are superior habitats because the amount and/or quality of nutrients translocated either to or from the leaf is correlated with leaf size. Probability of stem-mother failure, body weight of stem mother and progeny, number of progeny, development rate of progeny to maturity, and number of embryos in mature progeny are all correlated with leaf size. Due to these selection pressures, stem mothers search for and colonize large leaves with considerable accuracy.

Since selection pressures strongly favor those stem mothers which succeed in colonizing large leaves, an interesting choice is created. Once the largest leaves are occupied by individual stem mothers, what are the alternatives for unsettled individuals? Should the colonizing stem mother displace potential competitors, should she colonize the next largest leaf size available, or should she settle to become the second colonizer on the largest leaf already occupied? It is the intent of this paper to examine the basic model of habitat selection by quantifying the resultant fitnesses achieved by individual stem mothers in habitats they selected.

METHODS

This paper is concerned with the portion of the *Pemphigus* life cycle spent on the primary host. Analyses of the secondary host have not been included. This, however, does not detract from the overall results because, regardless of events occurring on the secondary host, individual colonizers should settle on the primary host in a way which maximizes their reproductive success. Since variation in suitability can be great within and between trees (Whitham 1978, unpublished data), all 526 galls examined were randomly sampled from the lower 4 m of a large branch of a single tree to ensure that all aphids had encountered the same potential plant defenses. In addition to the gall collections made in 1975, observations on colonizing behavior in early spring were made on nearby trees in 1975, 1976, and 1978. All trees were located at the edge of the Weber River near Ogden, Utah.

Since galls are initiated on immature leaves at bud burst, only those leaves produced during the initial flush of spring growth (early leaves) are available for colonization. Only these leaves were considered in this study. The aphid habitat was defined as an individual leaf, and habitat quality was quantified as leaf surface area. Greatest length times greatest width of mature leaves was used as an accurate correlate of actual leaf area ($r = 0.998$, $N = 27$, $P < .001$). Actual leaf area was measured by tracing representative leaves on finely lined paper and summing the number of 1 mm^2 within the leaf outlines. By using the linear equation, $Y = .624X + .127$, all length-times-width measurements were converted into leaf areas.

Competitor density within a habitat was measured as the number of galls per leaf, which is equivalent to the number of colonizing stem mothers. Stem mothers

which fail to successfully colonize a leaf and die a few days after bud burst leave a small identifiable scar or aborted gall on the leaf (Whitham 1978). Even stem mothers which abandon one leaf and move to another produce either one successful or one aborted gall. Thus, a census of aborted and successful galls accurately reflects the number of stem mothers that survive dispersal from the tree trunk to developing leaf buds. Throughout this paper the term gall is used in reference to the colonizing attempts of both successful and unsuccessful stem mothers.

To study the reproductive success of individual stem mothers, galls were collected over a 4-day period (July 2–5) when stem-mother progeny were starting to mature. Since all galls were initiated on virtually the same day in spring (May 14), the data represent a cohort having the same developmental period, about 51 days. Small branches were randomly selected and the sizes of all galled and gall-free leaves were measured. The positions of all galls on the leaf blade were measured and galls were placed in 85% alcohol. Upon completing the random sampling, a tally was made to determine which data categories lacked sufficient information for analysis. For example, leaves with 3 or more galls represented only 4% of the total galls available, and additional sampling was necessary to fill out the distribution. Such data collection procedures account for differences in sample size in the following section of this paper. In the laboratory galls were examined for the presence of predators and number of progeny was counted. Stem mothers and winged migrants were oven dried, allowed to equilibrate to a relative humidity of 32% at 25° C, and individually weighed on a Cahn electrobalance.

DATA AND ANALYSIS

Leaf-Size Selection

By combining several measures of reproductive success from data of Whitham (1978), failure rate, number of progeny, and number of embryos in mature progeny, a conservative estimate of the selective advantage gained by being the only colonizer on a leaf which matures to a size $> 15 \text{ cm}^2$ is an increase in fitness 7.3 times greater than on a mature leaf $\leq 5 \text{ cm}^2$. Such differential reproductive success accounts for the observation that stem mothers settle nonrandomly on leaves of varying size. Figure 2 shows that even though small leaves are abundant few are colonized, and large leaves are occupied by one or more galls. On leaves $\leq 5 \text{ cm}^2$, which account for approximately 32% of all available leaves, only 3% were colonized. In comparison, on those leaves $> 15 \text{ cm}^2$, which represent only 1.6% of the total leaves available, all were colonized and the average leaf supported nearly 1.6 galls. Thus, the larger-leaf-size category is colonized at a rate approximately 50 times greater than the smaller-leaf-size category.

Because the number of stem mothers exceeds the number of optimal leaves in this study (35 stem mothers per 100 leaves), most are forced to either double up on the largest leaves or occupy smaller leaves singly. Colonizing stem mothers apparently respond to the presence of others by adjusting densities on leaves of different size. Although there is considerable overlap in the distributions, the

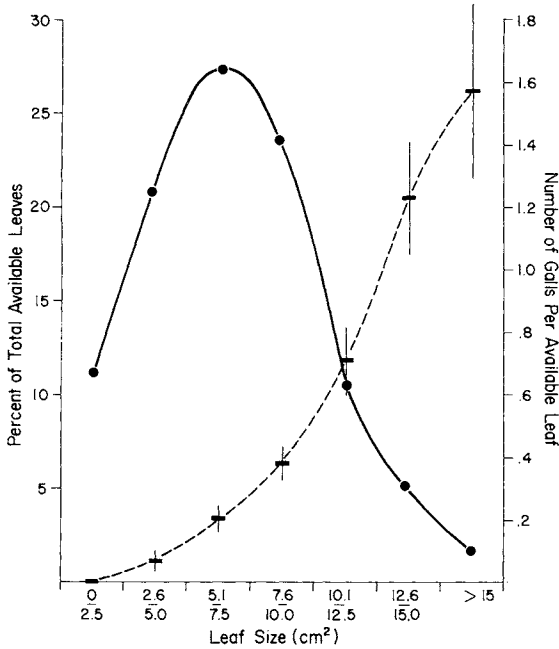


FIG. 2.—Solid circles = the distribution of leaf sizes available for colonization (mean leaf size = $6.9 \pm .17$ cm², $N = 422$); solid bars and vertical lines = means ± 1 SE of the number of galls per available leaf of each leaf size category (mean leaf size colonized = $10.9 \pm .27$ cm², $N = 153$). At a density of 35 stem mothers per 100 leaves, the mean leaf size colonized is 60% larger than the mean leaf size available.

mean size of leaves with one, two, three, and four galls increases by a fairly constant amount from 10.2 to 12.3 to 14.6 to 16.6 cm², respectively, and all are larger than the mean leaf size (6.9 cm²) available (table 1). In progressing from leaves with one gall to those with four galls, the incremental increase in leaf size is 2.1, 2.3 and 2.0 cm², respectively. These and other data suggest the use of some type of settling rule based upon leaf size and competitor density.

An alternative hypothesis to the selective settling of stem mothers argued so far is that stem mothers cause the leaf to become larger due to their feeding activities. Whitham (1978) examined the size of leaves with similar potential for becoming large and found no significant differences between galled and gall-free leaves. Thus, the feeding activities of these aphids do not affect mature leaf size.

Fitness as a Function of Habitat Quality and Competitor Density

If expected fitness is the basis for habitat selection, by examining the relative fitness of stem mothers in habitats of varying quality (leaf size) and competitor density (galls per leaf), the habitat selection process can be examined. One measure of stem mother relative fitness is the number of progeny contained within each gall. With *Pemphigus betae* leaf size accounts for 40%–60% of the variance in aphid numbers. Figure 3 shows a family of fitness curves for leaves of different

TABLE 1
MEAN LEAF SIZE AVAILABLE TO STEM MOTHERS
AND MEAN LEAF SIZES SELECTED

	Leaf Size (cm ²) Mean ± 1 SE	N	% of Total Galls
Leaf size of tree	6.9 ± .17	422	...
1 gall/leaf	10.2 ± .31	109	67
2 galls/leaf	12.3 ± .47	68	29
3 galls/leaf	14.6 ± .40	54	4
4 galls/leaf	16.6 ± .67	12	<1

NOTE.—ANOVA (Student-Newman-Keuls) yields significant differences ($P < .01$) for all means except leaves with three and four galls for which P is slightly greater than .05.

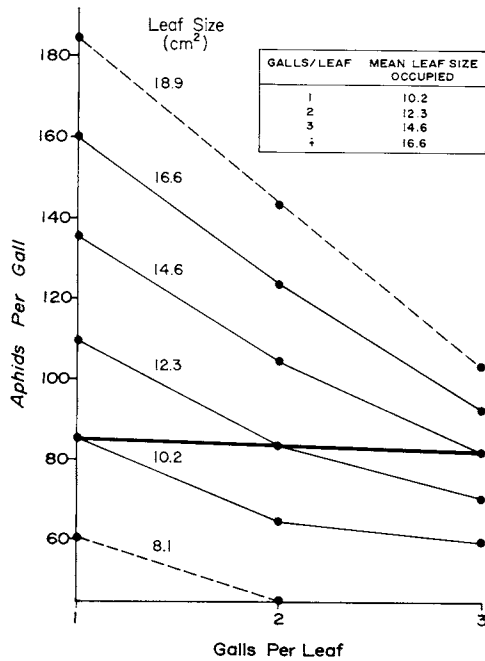


FIG. 3.—Family of fitness curves for habitats of varying quality (leaf size) and competitor density (galls per leaf). Points connected by solid narrow lines represent the expected fitnesses that would be achieved on the mean leaf sizes occupied by the various gall densities per leaf. Points connected by dashed lines represent expected fitnesses that would be achieved on the largest available leaves (18.9 cm²) and the smallest frequently colonized leaves (8.1 cm²). The number of aphids per gall not only increases with increased leaf size, but also decreases with increased competitor density. Points connected by the heavy horizontal line are unique because they represent the average fitnesses for one, two, and three stem mothers per leaf (see text).

sizes and galls per leaf. This figure is the result of three separate linear regressions of the number of progeny on leaves with one, two and three galls as a function of leaf size. Stem mothers that died (aborted galls) are included as having zero progeny. Points arranged vertically were predicted by substituting into each best-fit regression equation the mean leaf size occupied by one, two, three, or four galls per leaf (10.2, 12.3, 14.6, and 16.6 cm², respectively). The extreme in leaf size available and the smallest leaf size frequently colonized (18.9 and 8.1 cm², respectively) were treated in identical fashion. Thus, for various competitor densities (one to three galls per leaf), vertical examination of the three columns of predicted fitness values show how reproductive success changes with increased leaf size or habitat quality. Furthermore, by holding leaf size constant and allowing competitor density to increase from one to three galls per leaf (points connected by narrow dashed lines or narrow solid lines), the effect of competitor density on reproductive success can be examined. The points connected by the heavy horizontal line are unique because they represent the average reproductive success actually achieved on leaves with one, two, or three galls per leaf.

Three major points are demonstrated in figure 3. First, for any competitor density, as habitat quality increases average fitness also increases. For example, with one gall per leaf, as leaf size increased from 8.1 to 18.9 cm² the average number of aphids per gall more than tripled. Second, if habitat quality is held constant, as the number of competitors increases average fitness declines. On leaves measuring 18.9 cm², as the density of stem mothers increased from one to three the average number of aphids per gall declined from 185 to 102. The fact that increased stem-mother density within a habitat negatively affects fitness confirms that stem mothers compete intraspecifically. Third, stem mothers have adjusted their densities in habitats of varying quality such that the average fitness in habitats with several competitors is equal to the average fitness in habitats with none. The average number of aphids per gall is nearly the same for one, two, and three galls per leaf (depicted as heavy horizontal line in fig. 3). The average number of aphids per predator-free gall \pm 1 SE for a random sample of leaves with one gall each = 79 ± 8.4 , $N = 85$; 2 galls per leaf = 84 ± 6.3 , $N = 102$; 3 galls per leaf = 81 ± 7.4 , $N = 87$; and 4 galls per leaf = 73 ± 13.0 , $N = 28$. Leaves with four galls are not shown graphically because sample size (seven leaves with four galls each) was insufficient for regression analysis. Analysis of variance (Student-Newman-Keuls, SNK) reveals no significant differences between means ($P \gg .05$). These means are slightly different than those plotted in fig. 3 because galls with predators were included in calculating the mean leaf sizes occupied but were not used in measures of reproductive success. Effects of predation of fitness are examined later in this paper.

Although the average number of progeny per gall on leaves of different quality and competitor density is equal and thus appears to confirm the "free distribution" model of habitat selection, other measures of relative fitness such as body weight, abortion rate, development rate, and predation rate may not be equal. Analyses of these other measures of relative fitness produce results identical to those already detailed in examining the number of progeny per gall (fig. 3).

Using the same graphical analysis employed in figure 3, figure 4 examines how

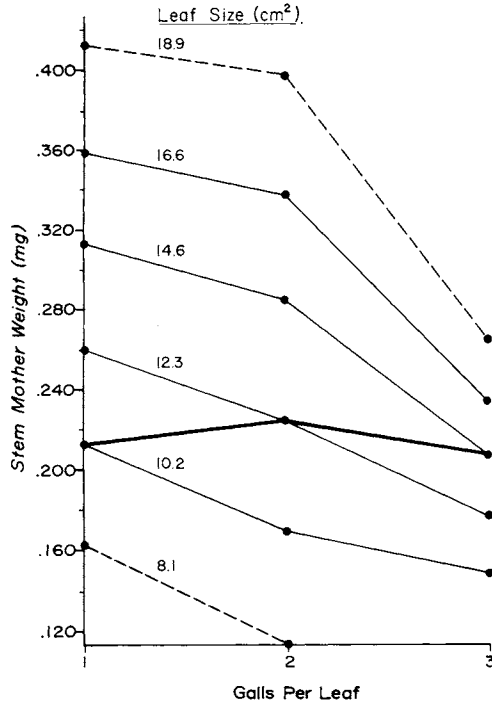


FIG. 4.—Dry body weight of stem mothers is shown for habitats of different quality and competitor density. Methods of analysis and results are identical to those in fig. 3.

dry body weight of mature stem mothers is affected by leaf size and stem-mother density. Stem mothers which aborted are included as having zero body weight. Whitham (1978) showed that large stem mothers produced more progeny, which when mature were larger and contained more preformed embryos than small stem mothers. Notice that the results shown in figure 4 parallel those of figure 3. If density is held constant, as leaf size increases stem-mother dry body weight increases. If leaf size is held constant and density increases, average weight declines. Finally, the heavy horizontal line shows that the average body weights are very similar for leaves with one, two, and three galls. The mean dry body weight ± 1 SE for a random sample of leaves with 1 gall each = $.201 \pm .0196$ mg, $N = 85$; 2 galls per leaf = $.233 \pm .0147$ mg, $N = 102$; 3 galls per leaf = $.208 \pm .0158$ mg, $N = 87$; and 4 galls per leaf = $.191 \pm .0289$ mg, $N = 28$. Again, analysis of variance (SNK) demonstrates no significant differences ($P \gg .05$).

Another measure of relative fitness is the number of stem mothers that die attempting colonization and leave only an aborted gall or scar as evidence of their presence. Figure 5A shows the percent stem mothers that died as a function of mature leaf size. Only leaves with one gall were included. Of those stem mothers attempting colonization on the smallest leaves, 80% died, while 0% failed on the largest leaves. Thus, with constant competitor density, as leaf size increases the probability of failure declines. Furthermore, if leaf size is held constant, increases

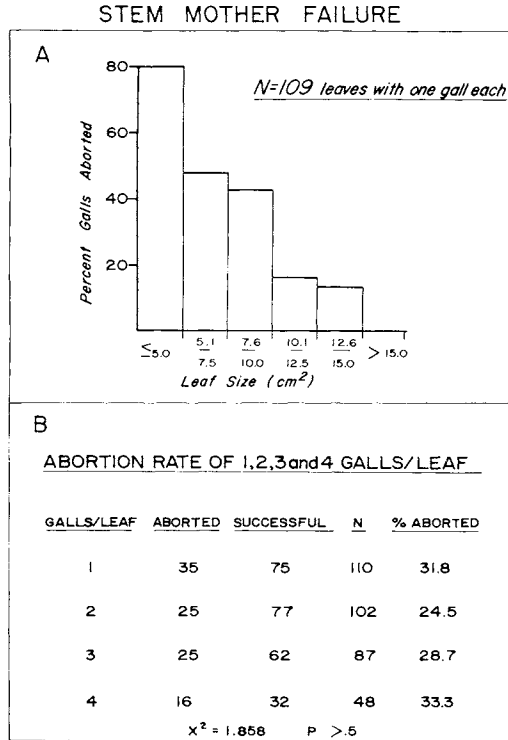


FIG. 5.—A, Percent stem mothers that die as a function of leaf size colonized. At a constant competitor density of one gall per leaf, stem mothers that die early in gall development are most likely to be found on small leaves. B, The advantages of colonizing large leaves are negated by increased competitor density such that the failure rates of stem mothers on leaves with one, two, three, and four galls are not significantly different.

in stem mother density result in increased failure rates. For example, on leaves greater than 15 cm² with one gall per leaf 0% failed, whereas 22% failed on leaves with three galls. This trend has been confirmed using Page's analysis of variance for ordered alternatives ($P < .05$, $N = 280$ galls; Hollander and Wolfe 1973). If stem-mother densities are adjusted in response to expected fitness as previous data indicate, then the probability of failure on leaves of different competitor density should be equal. Figure 5B shows that there are no significant differences in the failure rates of stem mothers on leaves with one, two, three, or four galls.

Yet another measure of relative fitness is the rate at which progeny mature to adults (winged migrants). This is important because progeny which mature first and migrate from the host tree escape rising predation rates. At the time when most galls contain winged migrants, as many as 60% of all surviving (nonaborted) galls may contain predators. The progeny of stem mothers on large leaves mature sooner than those on small leaves. Only leaves with single, surviving, and predator-free galls were examined after each had the same developmental period. The mean leaf size occupied by galls containing only immatures measured $7.4 \pm$

TABLE 2
EFFECT OF GALL DENSITY ON THE GROWTH OF
IMMATURES TO ADULT MIGRANTS

Galls per Leaf	Galls Without Winged Migrants	Galls With Winged Migrants	% Galls With Winged Migrants	N
1	14	41	74.5	55
2	23	59	72.0	82
3	15	60	80.0	75
4	1	13	92.9	14

NOTE.— $\chi^2 = 3.660$, $P > .29$; aborted galls not included.

.63 cm² ($N = 35$), while the mean leaf size of galls with adults was 55% larger and measured $11.5 \pm .49$ cm² ($N = 73$; $t = 4.971$, $P < .001$). Thus, with constant competitor density (one gall per leaf), an increase in leaf size results in a faster rate of development to maturity. Stem mothers also adjusted their densities on leaves of different size such that leaves with one, two, three, or four galls are equally likely to contain adult migrants (table 2). Again, this is consistent with results obtained with other measures of relative fitness.

Since predators do not selectively forage in a predictable pattern, it appears that predators have no effect upon the habitat selection process. Assuming that the use of clumped resources results in greater foraging efficiency, predators might forage on large, multiple-galled leaves more frequently than on small leaves with a single gall. If this is the case, predators could be an important factor in the settling decision of stem mothers and could negate the effects of habitat quality and competitor density previously examined. Some of the most common predators on *Pemphigus* aphids are two dipteran larvae, *Syrphus bigelowi* and *Leucopis pemphigae*, and adults and nymphs of the hemipteran, *Anthocoris* sp. (Harper 1959, 1963; Grigarick and Lange 1967). Due to a small sample of randomly collected predator-free and predator-infested galls, analysis of leaves with three or four galls was not possible. However, on leaves with one or two galls which account for 96% of all galls available, the probability of an individual gall being preyed upon did not differ significantly for leaves with either 1 or 2 galls ($\chi^2 = .045$, $P > .8$). On leaves with 1 gall, 30.8% were infested with predators ($N = 65$) compared with 28.6% ($N = 28$) on leaves with two galls (only nonaborted galls included). Furthermore, with constant prey densities (one gall per leaf), predators do not selectively forage on the largest leaves where prey reproductive success is greatest (Whitham 1978). The lack of discrimination by predators may result from the fact that clumped resources are far less common than dispersed resources (table 1). Therefore, from the predators' viewpoint, leaves with many galls are less favorable because they may be more difficult to locate.

This section has examined five measures of relative fitness: number of progeny per stem mother, body weight of stem mothers, abortion rate, development rate and predation. The results indicate four basic conclusions. (1) Increased habitat quality, i.e., leaf size, results in increased fitness. (2) The colonization of suboptimal habitats due to high stem mother densities and the decline in average fitness

with increased stem mother density are results of intraspecific competition. (3) Stem mothers react to habitat quality and competitor density by colonizing large leaves and doubling up on the largest leaves. (4) The average fitnesses of one, two, three and four galls per leaf were in most cases nearly identical. Identical results for five measures of fitness represent strong evidence that stem mothers have adjusted their densities in habitats of different quality such that the average fitness in habitats with a high density of competitors is the same as in habitats with fewer competitors.

Unequal Expected Fitnesses and Territoriality

Although data presented in this paper appear to strongly support the "free-distribution" model of habitat selection (fig. 1), critical assumptions built into the analytical model are violated. Since dominance and/or territoriality are not exhibited by individuals in the free distribution, no colonizer can prevent another from settling and using available resources. Thus, as additional colonizers settle within a habitat, expected fitnesses of all individuals are reduced by an equal amount and all have the same expected fitness. In comparison, with the "despotic distribution" dominance and/or territoriality should prevent settling of subdominants and cause expected fitness within the habitat to be unequal. The following results show that *Pemphigus betae* exhibits territorial behavior and that within a habitat expected fitnesses are unequal. Both of these results are characteristic of the despotic distribution.

Due to the effect of gall position on reproductive success, expected fitnesses within the leaf habitat are not equal. When two or more stem mothers settle on the same leaf blade they arrange themselves linearly along the midrib. Figure 6 shows that on multiple-galled leaves gall position has a tremendous effect on fitness. Stem mothers at the base of leaves enjoy far greater success than stem mothers more distally located. For example, on leaves with three galls the probability of dying during the colonization attempt increases from 3.5% at the base to 62.1% in the most distal position ($\chi^2 = 25.708$, $df = 2$, $P \ll .001$). Similarly, mean number of progeny per stem mother and stem-mother dry body weight are greatest in the basal gall position (ANOVA Student-Newman-Keuls, $P < .01$ for all means of both progeny and weight). Stem mothers which died in the colonization attempt and left aborted galls are included as having zero progeny and weight. Using survivors only, the same trends hold. Comparing means of surviving stem mothers at the base of the leaf with those most distal (three galls per leaf) shows that basal galls contain 90% more progeny and stem mothers are 34% heavier (analysis of variance Student-Newman-Keuls, $P < .01$ for both progeny and weight). Thus, not only does position affect survival during colonization and settling, but position affects the reproductive success of survivors as well.

An unexpected result shown in figure 6 is that stem mothers occupying the most heavily populated habitats (leaves with three galls) simultaneously achieved the highest and lowest measures of fitness. Stem mothers at the base of leaves with three galls (T_1) achieved the highest reproductive success, the most distal position (T_3) had the lowest success, and all other gall densities and positions (S, D_1, D_2, T_2)

EFFECT OF POSITION ON FITNESS

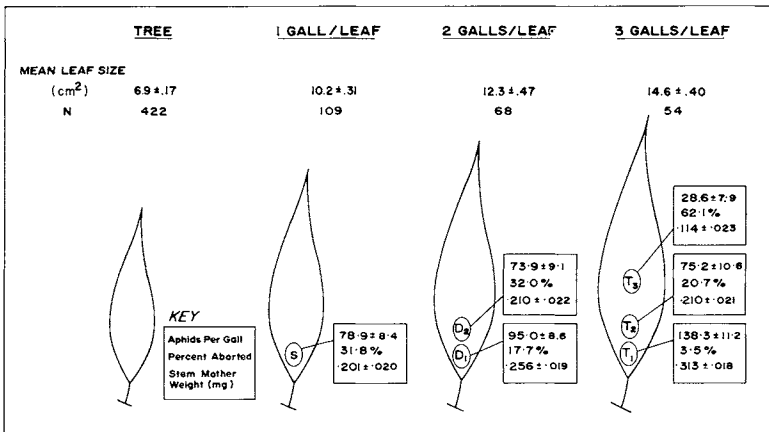


FIG. 6.—Gall position on the leaf blade has a tremendous effect on fitness. Stem mothers distally located have fewer progeny, greater probability of failure, and lower dry body weight. Leaves are drawn to scale and galls are accurately positioned on the leaf blade. Means \pm 1 SE are shown.

had intermediate success. This condition is similar to that found in territorial animals where subdominants or less aggressive individuals are forced into the marginal areas of the breeding habitat. Although their fitness is greatly reduced, it is still greater than if they had not settled at all.

Since the basal position of leaves results in greater reproductive success, it is not surprising that when two stem mothers occupy the same leaf blade the basal stem mother actively defends her position (Whitham 1979). Behavioral interactions are limited to the few days when stem mothers are searching for suitable leaves and first settling. Soon after settling expanding leaf tissues isolate each stem mother within a hollow gall and prevent further physical contact. However, before stem mothers become isolated, aggressive interactions occur during which an intruder can successfully displace an established stem mother. These interactions are mediated through shoving and kicking contests which may last as long as 2 days; the largest stem mother usually wins the basal position. When competitor densities are high, territorial behavior can result in the production of a floater population of subdominants searching for places to settle (Whitham 1979).

Experiments demonstrate that when a dominant stem mother is removed from her superior territory at the base of the leaf blade a subdominant competitor may quickly move in to take over the vacated position. Figure 7 shows the results of a removal experiment in which the positions of two colonizing stem mothers were plotted as a function of time. When the basal stem mother was removed, the distal stem mother shifted down to occupy the more favorable basal position. This is precisely the result expected to occur in a competitive system when a dominant individual is removed from its territory. These results are similar to those obtained in other systems as diverse as birds, mammals, fish, and insects (Stewart and Aldrich 1951; Hensley and Cope 1951; Gerking 1953; Moore 1964; Healey 1967; Watson 1967; Smyth 1968; Krebs 1971). For insects, it should be pointed out that

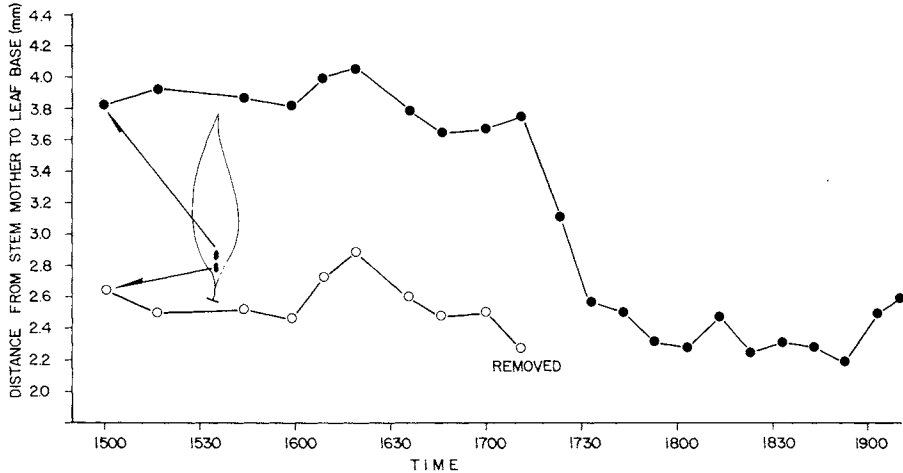


FIG. 7.—The positions of two colonizing stem mothers on one leaf blade are plotted as a function of time. Kicking and shoving contests sharply define the boundaries of each stem mothers's territory. Since the basal position is the most favorable, when the stem mother occupying this position is removed with a fine brush the distal stem mother shifts down to take over the most favorable position.

while territoriality and its underlying premise of competition for limited resources are greatly debated, evidence is accumulating which indicates that territoriality may be common in insect groups. Price (1975) cites 35 papers which deal with territoriality in eight orders of insects.

Heterogeneous Habitats

An assumption of both the free and despotic distributions, which is violated in this system, is that habitats are homogeneous. Since individual leaves are highly heterogeneous in suitability, this feature may account for the contradictory results of the previous two sections. The effect of gall position on fitness (fig. 6) shows that not all portions of the leaf are equally suitable for colonization. Furthermore, when there is only one *Pemphigus betae* gall per leaf, gall position has a significant effect on fitness (Whitham 1978); galls positioned distally on the leaf blade contained fewer progeny, which developed to maturity at a slower rate. This differential in reproductive success accounts for the observation that when there is just one gall per leaf nearly all are formed at the base of the leaf blade. Apparently settling in a distal position effectively reduces the size of the leaf from which the stem mother and her progeny draw resources.

DISCUSSION

Homogeneous and Heterogeneous Habitats

There is a tendency for field ecologists to fit their interpretations of data into existing theory (Dayton 1973). In the present study, had I proceeded no further

TABLE 3
 PREDICTIONS OF EXPECTED FITNESS IN HETEROGENEOUS
 AND HOMOGENEOUS HABITATS

Animal Behavior	Habitat Characteristics	Expected Fitness of Densest Habitat Compared to Less Dense Habitat	Expected Fitness of Individuals Within a Habitat
Territorial	Homogeneous	>	≠
Territorial	Heterogeneous	=	≠
Nonterritorial	Homogeneous	=	=
Nonterritorial	Heterogeneous	>	≠

NOTE.—Predictions of expected fitness in heterogeneous habitats from present paper; predictions of expected fitness in homogeneous habitats from Fretwell and Lucas (1970).

than the basic result that the average fitness of stem mothers in habitats with the highest density of competitors is equal to those occupying habitats with fewer competitors, theory would have been convincingly confirmed for the wrong reason. Obviously theoretical models developed around the assumption of homogeneous habitats are not directly comparable to empirical results obtained from field studies of heterogeneous habitats. However, since the latter is probably the general case in the field, it is of particular interest to know if the two are compatible.

If both theory and field results are correct, when a *territorial* animal shifts from a homogeneous to a heterogeneous habitat changes in predictions must be due to differences in habitat characteristics. Fretwell and Lucas (1970) predicted that for a territorial animal in a homogeneous habitat, due to the exclusion of less dominant competitors, average fitness would be *greatest* in habitats with the highest density of competitors. In comparison, the present study indicates that with the dominant behavior exhibited by stem mothers in heterogeneous habitats average fitnesses at varying competitor density are *equal* (table 3).

If the above change in predictions is due to habitat characteristics alone then, by applying the same assumptions of the models of Fretwell and Lucas (1970) to a *nonterritorial* animal shifting from homogeneous to a heterogeneous habitat, a similar change in predictions should occur. By assuming no territoriality and complete freedom to settle on any leaf, the first colonizers to arrive should settle at the base of the largest leaves while the later arrivals must decide whether to double up on an already occupied leaf or to colonize the base of a smaller unoccupied leaf. Since there is complete freedom to settle on any leaf, the *last colonizers to arrive* determine which leaves have one, two, three or four galls. This leads to the prediction that if the last colonizers settle on those remaining leaf sizes and positions where their expected fitness will be greatest, the resultant mean fitness of $S = D_2 = T_3 = Q_4$ (Q_4 = the fourth position on leaves with four galls). Since fitnesses increase from the distal to most basal gall position (see fig. 6), if the most distal positions (S, D_2, T_3, Q_4) have the same expected fitness, then the average fitness of stem mothers on leaves with four galls will be *greater* than those on leaves with fewer galls ($\bar{W}S < \bar{W}D_{1,2} < \bar{W}T_{1,2,3} < \bar{W}Q_{1,2,3,4}$). In comparison,

theory predicts that for the same nonterritorial animal in homogeneous habitats the average fitnesses in habitats of varying competitor density are *equal*. Thus, applying the same assumptions of theory to the present system, when a nonterritorial animal shifts from a homogeneous to a heterogeneous habitat the predictions change (table 3).

A similar approach in examining the changes in predictions for territorial animals is more difficult. If territoriality acts to limit density within a habitat, then the *most dominant* stem mothers should occupy the base of large leaves and determine which leaves have one or more galls. This is in striking contrast to the nonterritorial system just examined in which the last arrivals determined which leaves had one or more galls. Consequently, the settling patterns should be different. Since a dominant can prevent a competitor from settling (Whitham 1979), territoriality should tend to disperse the population and increase the frequency of stem mothers occurring singly on large leaves. Thus, if the result of territoriality is to increase the size of leaves with one gall relative to multiple-galled leaves, then the expected rank in fitnesses would be $S > D_2 > T_3 > Q_4$. This would be consistent with observed results in which the number of progeny of $S = 79$, $D_2 = 74$, $T_3 = 29$, and $Q_4 = 0$. Until more is known about the fate of subdominants, however, this interpretation is speculative.

Although the above comparisons of heterogeneous and homogeneous habitats are not conclusive, they suggest that the results obtained from the habitat selection behavior of *Pemphigus betae* represent a logical extension of theory. Furthermore, since predictions of expected fitness in heterogeneous and homogeneous habitats can be identical for very different animal behaviors (table 3), if the assumption of habitat homogeneity is made without verification, as is frequently done, one may obtain the right answer for the wrong reason. Further studies may predict the extent to which habitat heterogeneity will favor behavioral changes and an altering of the habitat selection process.

Further Considerations

This study questions the existence of homogeneous habitats. All leaves on a tree are not equal in suitability, and even various positions on a single leaf produce significant differences in reproductive success. If habitats are restricted to homogeneous units, then the habitat is so small that only one gall can occupy the space. Thus, it becomes difficult to examine the effects of competitor density on habitat selection because competitor density within the habitat is always one. Furthermore, the presence of a second gall on the leaf blade negatively affects the fitness of the basal gall, causing it to have fitness lower than if it were the only gall on the leaf. If there is any biological basis for defining a habitat, it would seem logical to include within a habitat those adjacent units of the environment which may vary and significantly affect fitness. Using this definition, an individual leaf as a heterogeneous habitat is the smallest resource unit that could be defined as a habitat.

One of the most unsubstantiated assumptions of evolutionary ecology is that organisms have "ideal" behavior which enables them to maximize fitness. This assumption is rarely examined, and little is known about how deviations from the

ideal condition affect the validity of models. Using data of the present study, stem mothers realized at least 84% of their potential fitness (Whitham, in prep.). Potential fitness was calculated by allowing stem mothers unlimited search time, complete freedom to settle in the habitat of their choice (free distribution), and perfect response to habitats of varying quality and competitor density. This estimate is probably conservative because search time is not unlimited and territorial behavior prevents stem mothers from settling on any leaf or leaf gall position. If these factors could be included, stem mothers should achieve more than 84% of their potential fitness. Regardless of the specific mechanism employed by stem mothers to select superior habitats, this level of precision indicates that they effectively assess and integrate the variables of individual habitat quality, the distribution of habitat qualities, and the density of competitors in each habitat. Most importantly, it suggests that expected fitness is the basis for habitat selection. In a laboratory study, Mitchell (1975) showed that bruchid beetles possessed similar abilities in their selection of mung beans for oviposition sites and achieved 70% of their potential fitness. As high as these estimates appear to be, it is difficult to establish the required level where the "ideal" assumption is fulfilled.

SUMMARY

The gall-producing aphid *Pemphigus betae* is a plant parasite which colonizes the leaves of narrowleaf cottonwood, *Populus angustifolia*. Habitat quality and aphid fitness can be quantified easily, and one may census not only those colonizers which succeed in reproduction but also those which die attempting colonization. Using five measures of relative fitness and other data, selection pressures which drive the habitat selection process have been quantified. (1) Colonizing stem mothers have evolved the ability to discriminate and select only the best habitats for colonization. (2) As competitor density within a habitat increases, average fitness declines. Stem mothers settle in habitats of varying quality such that as habitat quality increases the density of competitors increases. (3) An individual leaf is a highly heterogeneous habitat. Position within the habitat has a predictable and pronounced effect on fitness. Due to position, the best habitats produce individuals with the highest and lowest fitness. (4) Because the number of optimal positions and best habitats can be low relative to the number of competitors, and since fitness declines as density increases, stem mothers have evolved territorial behavior which acts to limit density. (5) Identical results from five measures of relative fitness indicate that stem mothers adjust their densities in habitats of varying quality such that the average fitness of stem mothers in habitats with the highest density of competitors is the same as those occupying habitats with fewer competitors. (6) Theory of habitat selection has been restricted to animals exhibiting territorial and nonterritorial behavior in homogeneous habitats. This study empirically extends theory to consider the more general condition of heterogeneous habitats. (7) Assumptions of habitat homogeneity should not be made without verification because predictions of expected fitness in heterogeneous and homogeneous habitats can be identical for very different animal behaviors.

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LITERATURE CITED

- Brown, J. L. 1969. The buffer effect and productivity in tit populations. *Am. Nat.* 103:347-354.
- Dayton, P. K. 1973. Two cases of resource partitioning in an intertidal community: making the right prediction for the wrong reason. *Am. Nat.* 107:662-670.
- Doyle, R. W. 1975. Settlement of planktonic larvae: a theory of habitat selection in varying environments. *Am. Nat.* 109:113-126.
- Fretwell, S. D. 1972. *Populations in seasonal environment*. Princeton University Press, Princeton, N.J.
- Fretwell, S. D., and H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19:16-36.
- Gerking, S. D. 1953. Evidence for the concepts of home range and territory in stream fishes. *Ecology* 34:347-365.
- Grigarick, A. A., and W. H. Lange. 1967. Seasonal development and emergence of two species of gall-forming aphids, *Pemphigus bursarius* and *P. nortoni*, associated with poplar trees in California. *Ann. Entomol. Soc. Am.* 61:509-514.
- Grinnell, J. 1914. Barriers to distribution as regards birds and mammals. *Am. Nat.* 48:248-254.
- . 1922. The role of the "accidental." *Auk* 39:373-380.
- Harper, A. M. 1959. Gall aphids on poplar in Alberta. II. Periods of emergence from galls, reproductive capacities, and predators of aphids in galls. *Can. Entomol.* 91:680-685.
- . 1963. Sugar-beet root aphid, *Pemphigus betae* Doane (Homoptera: Aphididae) in southern Alberta. *Can. Entomol.* 95:863-873.
- Healey, M. C. 1967. Aggression and self-regulation of population size in deer mice. *Ecology* 48:377-392.
- Hensley, M. M., and J. B. Cope. 1951. Further data on removal and repopulation of the breeding birds in a spruce-fir community. *Auk*:483-493.
- Hollander, M., and D. A. Wolfe. 1973. *Nonparametric statistical methods*. Wiley, New York.
- Krebs, J. R. 1971. Territory and breeding density in the great tit, *Parus major* L. *Ecology* 52:2-22.
- Kluyver, H. N., and L. Tinbergen. 1953. Territory and the regulation of density in titmice. *Arch. Neerl. Zool.* 10:265-289.
- Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, London.
- Levins, R. 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *Am. Nat.* 96:361-373.
- . 1968. *Evolution in changing environments*. Princeton University Press, Princeton, N.J.
- MacArthur, R. H. 1972. *Geographical ecology*. Harper & Row, New York.
- Mitchell, R. 1975. The evolution of oviposition tactics in the bean weevil, *Callosobruchus maculatus* (F.). *Ecology* 56:696-702.
- Moore, N. W. 1964. Intra- and interspecific competition among dragonflies (Odonata): an account of observations and field experiments on population control in Dorset, 1954-60. *J. Anim. Ecol.* 33:49-71.

- Price, P. W. 1975. Insect ecology. Wiley, New York.
- Rosenzweig, M. L. 1974. On the evolution of habitat selection. Proc. 1st Int. Congr. Ecol. 401-404.
- Smyth, M. 1968. The effects of removal of individuals from a population of bank voles (*Clethrionomys glareolus*). J. Anim. Ecol. 37:167-183.
- Stewart, R. E., and J. W. Aldrich. 1951. Removal and repopulation of breeding birds in a spruce-fir forest community. Auk 68:471-482.
- Templeton, A. R., and E. D. Rothman. 1974. Evolution in heterogeneous environments. Am. Nat. 108:409-428.
- Watson, A. 1967. Population control by territorial behavior in red grouse. Nature (Lond.) 215:1247-1275.
- Wiens, J. A. 1976. Population response to patchy environments. Annu. Rev. Ecol. Syst. 7:81-120.
- Whitham, T. G. 1978. Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. Ecology 59:1164-1176.
- . 1979. Territorial behavior of *Pemphigus* gall aphids. Nature (Lond.) 279:324-325.